

Ectoparasite burden influences the denning behavior of a small desert carnivore

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Abstract. Quantifying the impacts of parasitism on a host can be arduous and is generally understudied for ectoparasites, with known works being either laboratory-focused, correlational-based, or only focusing on a few species and spatial extents. Many mammalian species have evolved the modality of denning behavior, a lifestyle that can lead to higher ectoparasite burden, and it has been posited that animals may alter their denning behavior in an attempt to reduce exposure to ectoparasites. We conducted a test of the ectoparasite release hypothesis for kit foxes (*Vulpes macrotis*) and fleas in the Great Basin Desert of the western United States, a hypothesis that has remained relatively untested for over half a century. We experimentally administered a flea reduction treatment to a subset of kit foxes. We then measured and compared the number of unique den usages and residency time across treatment and control foxes (no flea reduction treatment) while accounting for other factors known to influence denning behavior. Foxes treated with the flea medication reduced the number of unique dens and increased their residency times at dens. All kit foxes continued to use multiple dens on the landscape, suggesting several factors in addition to flea burden influence denning behavior. Our results confirm the long-dormant ectoparasite release hypothesis and suggest ectoparasites may shape the behavior of burrowing vertebrates to a greater extent than previously recognized.

Key words: denning; ectoparasite release hypothesis; flea; Great Basin Desert; kit fox; telemetry; *Vulpes macrotis*.

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INTRODUCTION

A central goal of ecology is the identification of species interactions and the consequences thereof. Notable types of species interactions, including predation, competition, and parasitism, can have individual-level (e.g., behavior, survival) and population-level impacts (e.g., species distribution, abundance, occupancy) on a myriad of species (Thompson 1999, Davies et al.

2012, Lonsinger et al. 2017). Of these, host–parasite interactions can be strong determinants of host behavior and fitness with cascading effects on their population dynamics and distribution (Booth et al. 1993, Hatcher and Dunn 2011, Sponchiado et al. 2017). Direct (nonpathogenic) impacts of ectoparasites on hosts are largely understudied compared to those of endoparasites (Moore 1984, Dobson 1988, Hudson et al. 1998, Pedersen and Greives 2008, Tompkins et al.

2011). Yet, a growing body of research on ectoparasites reveals they can influence energy budgets (Giorgi et al. 2001, Kam et al. 2010), number of offspring (Neuhaus 2003), behavior (Mooring and Samuel 1999, Scantlebury et al. 2007), and survival (Hawlena et al. 2006) of their hosts. These effects can occur through the direct effects of hematophagy and inflammation caused by flea bites (e.g., Hawlena et al. 2006), or indirectly through disease transmission (Thompson 1999).

Similar to the invasive species centered enemy release hypothesis (ERH), the ectoparasite release hypothesis (EPRH) predicts that a host species will benefit when ectoparasite enemies (e.g., native fleas) are no longer present or markedly reduced (Keane and Crawley 2002, Zwolak et al. 2013, Mlynarek 2015). While ERH has been widely studied (Colautti et al. 2004, Torchin and Lafferty 2009, Schultheis et al. 2015), EPRH investigations are sparser, often laboratory-based (Hawlena et al. 2006, Devevey et al. 2008, Devevey and Christe 2009) or strictly observational in nature (Zwolak et al. 2013). Works on EPRH incorporating a known or assumed experimental reduction of ectoparasites under field conditions have occurred (Butler and Roper 1996, Roper et al. 2002, Biggins et al. 2010, Hillegass et al. 2010, Matchett et al. 2010, Krams et al. 2013, Gladalski et al. 2018), but are limited to a few species and investigated metrics, (e.g., apparent survival, den-complex use, animal health as derived from serology). For example, to our knowledge no investigations have examined whether ectoparasites influence denning behavior of mammalian carnivores that regularly utilize den sites distributed widely across a given landscape. Consequently, additional manipulation-based field investigations are needed to both gain a better general understanding of EPRH and elucidate the role ectoparasites can play on host individuals and populations (Zwolak et al. 2013).

A suite of factors can influence presence and severity of ectoparasites on hosts (Wall and Shearer 2001, Hatcher and Dunn 2011). In mammals, denning behavior, and the accompanying semi-fossorial lifestyle, is a modality often leading to increased ectoparasite presence and burden (Butler and Roper 1996, Kinlaw 1999, Roper et al. 2002, Archer et al. 2016). Denning behavior is commonly exhibited in desert-adapted species

to reduce the energetic costs associated with thermoregulation and thermal conductance, and to mitigate predation risk (Kinlaw 1999). For denning mammals, the use of multiple dens on the landscape or within an individual's territory has been observed for several desert-adapted species (Kinlaw 1999, Louw et al. 2017) and is especially common in mammalian carnivores (Linnell et al. 1999, Anderson and Richardson 2005, Phelan and Sliwa 2005). Importantly, dens also provide suitable environmental conditions for the persistence and reproduction of fleas (Beck and Pfister 2004, Salkeld et al. 2007) that, in turn, can strongly influence host behavior and fitness (Zwolak et al. 2013).

Over 55 yr ago, Egoscue (1962) observed kit foxes (*Vulpes macrotis*) utilizing an inordinate number of dens and hypothesized that heavy flea infestations within these dens were responsible for the high number of dens used by foxes. This behavior by hosts (i.e., increased number of dens used and decreased residence time in each den) reduces the exposure of individual foxes to high ectoparasite loads and allows parasite loads inside dens to decline between visits. Fleas are intermittent parasites, which can persist for an intermittent amount of time off their hosts under suitable environmental conditions (Zwolak et al. 2013), such as those provided by kit fox burrows (Salkeld et al. 2007). Further, larval and pupal development of fleas takes place off host, often in burrows (Beck and Pfister 2004). Thus, burrows regularly utilized by kit foxes are likely to contain more fleas than those relied upon less often. While patterns of den use by kit foxes have been studied throughout their range (Koopman et al. 1998, Rodrick and Mathews 1999, Arjo et al. 2003), the role of fleas in den use behavior, and consequently the hypothesis put forth by Egoscue (1962) over fifty years ago, remains untested for this native mesocarnivore.

Here, we describe an experimental manipulation of ectoparasite burden in kit foxes. Our objective was to test a specific and latent EPRH put forth by Egoscue (1962) that kit fox den use is influenced by flea burdens. We predicted the total number of unique dens used by each fox would be reduced for treatment animals. We also predicted that den residency time, the number of consecutive weeks a fox used a unique den, would be higher for treatment foxes.

MATERIALS AND METHODS

Study area

We conducted our research in the Great Basin Desert on the eastern portion of U.S. Army Dugway Proving Ground (DPG) and adjoining federal lands, Tooele County, Utah, USA. Elevations ranged from 1302 to 2137 m. Average annual long-term (1953–2009) and study-duration (2010–2013) temperatures derived from monthly mean maxima were 17°C (range 11°–21°C) and 17°C (range 15°–19°C), respectively. Long-term and study-duration annual precipitation averaged 24.5 cm (range 7.9–42.3 cm) and 18.1 cm (range 8.0–26.6 cm; National Oceanic and Atmospheric Administration, National Centers for Environmental Information; <https://www.ncdc.noaa.gov/data-access>). The terrain consisted of isolated small mountains, a portion of the Cedar Mountains, sand dunes, and alkaline flats that were dominated by black greasewood (*Sarcobatus vermiculatus*), big sagebrush (*Artemisia tridentata*), and juniper (*Juniperus osteosperma*) (Dempsey et al. 2014). Where wildfires had occurred, 40% of historical juniper woodland and shrub communities had been replaced by exotic herbaceous vegetation (Emrick and Hill 1999).

Capture and den use monitoring

Between March 2010 and November 2013, we captured kit foxes via road-based transect trapping (Schauster et al. 2002, Dempsey et al. 2014) and at known den sites (Kluever et al. 2013, Dempsey et al. 2014) using box traps (25 × 25 × 80 cm; Model 107; Tomahawk Live Trap, Hazelhurst, Wisconsin, USA) baited with hot dogs. At each capture, we weighed, determined sex, and aged individuals as juveniles (<12 months old) or adults (>12 months) based on tooth wear, tooth eruption, and body size (Kozlowski et al. 2008). We also combed each kit fox from nose to tail for 2 min to count and collect ectoparasites. Flea counts served as an index of kit fox flea burden (Archer et al. 2014). Collected fleas were stored in 100% ethanol and later hydrated, clarified in 10% KOH, dehydrated in ethanol, cleared in xylol, and mounted in Canada balsam on microscope slides for identification (Pigage et al. 2017). Processing and identification of fleas took place at the University of Colorado, Department of Biology, Colorado Springs, Colorado, USA.

We used a random number generator to assign 33% of captured kit foxes to the flea reduction treatment. This allowed us to implement an asymmetrical design where our control group (i.e., foxes not administered a flea reduction medication) outnumbered treated foxes; this framework has been recommended for field investigations that incorporate a manipulation component (Underwood 1994). For foxes assigned to the treatment group, we administered Frontline Plus For Dogs (TM), at a dosage of 0.67 mL (Merial, Duluth, Georgia, USA). Frontline Plus (TM) has been shown to effectively reduce ectoparasite burden in felids and canids for up to 14 weeks (Everett et al. 2011, Rohdich et al. 2014). On average, individual kit foxes were captured on 2.47 occasions (median = 2, SD = 3.41, range = 1 to 25; Kluever and Gese 2017). This allowed us to count fleas on multiple occasions for several individual foxes.

Prior to each release, we fitted each kit fox with a 30–50 g radiocollar (Model M1930; Advanced Telemetry Systems, Isanti, Minnesota, USA) weighing <5% of body mass. We located kit foxes >3 times per week using a portable receiver (Model R1000; Communications Specialists, Orange, California, USA) and a handheld 3-element Yagi antenna (Dempsey et al. 2014). We temporally distributed telemetry sampling by collecting 2 nocturnal locations and 1 denning location each week. Collecting weekly den locations provided us a count of unique dens utilized per unit time for each fox. Radio-telemetry was supplemented by regular use of infrared motion sensitive cameras (Kluever et al. 2013) in order to determine when juvenile foxes were large enough to be captured.

Study design and data analyses

We tested whether foxes in the treatment group exhibited reduced flea burden by comparing flea counts of individual foxes prior to and after receiving flea medications based on opportunistic recaptures of previously treated foxes. We constrained this comparison only to pre- and post-treatment flea counts that took place within 60 d of one another. We employed a 2-tailed permutation test with 20,000 resamples (Manly 2006) to test for differences in flea burden. Permutation tests are distribution-free in the sense that probabilities of obtaining extreme test statistic values given the truth of the null hypothesis

(type I errors) are based on permutations of the data from randomization theory and are not based on an assumed population distribution (Manly 2006). Permutation tests were performed using the coin package in R. For all statistical tests, we interpreted P-values in terms of relative evidence of differences (Ramsey and Schafer 2002).

We focused our den usage analysis on two complementary measures of den use behavior: (1) the total number of unique dens used by each fox in each season, and (2) the probability that a fox switches dens between successive weeks, regardless of whether each den had been previously used. The first measure provides an index of the overall breadth of den use, whereas the second measure provides an index of den use constancy; a higher probability of switching dens from week to week results in lower den use constancy. We chose this framework because Egoscue's (1962) EPRH predicted that kit foxes use more dens, and with lower constancy because flea loads are high.

We used a model selection approach to identify the dominant factors affecting each of these two response variables and to test the EPRH. For each response (number of unique dens and weekly probability of switching dens), we fitted a series of generalized linear mixed models (GLMMs) that included the explanatory covariates individually, in additive combinations, or with plausible pairwise interactions. We used Poisson GLMMs with a log link function to relate each covariate to the number of unique dens used by foxes (response 1). We confirmed the response variable was not over-dispersed ($P > 0.99$) using the dispersiontest function from the AER package in R (Kleiber and Zeileis 2009), which implements a formal test of mean–variance equality based on methods described in Cameron and Trivedi (1990). We used binomial GLMMs with a logit link function to relate covariates to the probability of switching dens from week to week (response 2). Explanatory covariates considered in models were flea treatment (a binary variable), study year (a categorical variable with four levels), season (breeding, pupping, and dispersal; Dempsey et al. 2014), and fox age (juvenile or adult). Sex was not included as a covariate because our limited number of data points restricted the number of

covariates we could include in our models. Fox identity was included as a random effect in all models, though models describing number of unique dens that included random effects were singular (i.e., random effect variance was estimated as zero). Following Pasch et al. (2013), random effects were subsequently omitted from those analyses, though we note that this does not influence estimates of fixed effects.

Preliminary analysis suggested the number of unique dens used per season was positively but non-linearly related to the number of times the fox was located, indicative of a strong sampling effort effect. Yet, this effect was negligible after the fox was located 10 times (see Appendix S1: Fig. S1). Thus, for models of this response variable we only included data for foxes that were located at least 10 times in a season (approx. 50% of data). For response 2 (weekly probability of switching dens), we limited our analysis to observations that occurred 7–14 d apart. If a fox was located in different dens in successive weekly observations, this was indicative of den switching and received a response value of 1 for that interval or 0 otherwise.

RESULTS

Captures, flea treatment, and den use

We captured 84 individual kit foxes (34 juveniles and 50 adults) and accumulated 234 seasonal den use observations. Seventeen of the den use observations consisted of foxes only being located once and were removed from consideration for analyses. Flea species encountered and identified, in order of prevalence, were *Pulex irritans*, *Meringis parkeri*, *Foxella ignota utahensis*, *Aetheca wagneri*, and *Peromyscopsylla hesperomys adelpha*; these species were similar to previous flea investigations for kit fox and congener species (Bossard 2006, Riner et al. 2018). Flea burden for foxes at onset of receiving flea medications averaged 15.4 (SE = 11.2) and ranged from 3 to 58 fleas, whereas flea burden for these treated animals subsequently recaptured within sixty days was 1.4 (SE = 0.4) and ranged from 0 to 5. The average number of days between pre- and post-treatment flea counts was 31 days (SD = 12.02). We found convincing evidence that flea counts differed pre- and post-treatment ($n = 26$, $P < 0.001$).

Number of unique dens used per season

The top model describing the number of unique dens used per season by each fox included only an effect of flea treatment (ΔAIC_c of null model that omitted this effect was 2.12). No other covariates were well-supported predictors of unique den usage (Table 1). Flea treatment reduced the number of unique dens used by foxes each season (Fig. 1; $P = 0.04$). Foxes that were administered flea medication used 3.3 dens per season (95% CI = 2.8–3.9), while untreated foxes used 4.1 dens per season (95% CI = 3.8–4.6).

Weekly probability of switching dens

The top model describing the weekly probability that foxes switch dens included an effect of flea treatment, as well as additive effects of season and age. All five top models included effects of flea treatment (Table 2), and models including flea treatment comprised 99.3% of model weights. Foxes that were administered flea treatment had lower weekly probabilities of switching dens than untreated foxes (Fig. 2; $P = 0.001$). The weekly probability of switching dens was higher for juveniles than adults ($P = 0.03$), and was highest during the breeding season (December 15–April 14), lowest during the pup-rearing season (April 15–August 14), and intermediate during the dispersal season (August 15–December 14). There was also considerable unexplained individual variation among foxes for weekly probability of den switching (individual random effect SD = 0.53 on logit scale).

Table 1. Covariate effects appearing in the top five models describing the number of unique dens used by kit foxes.

Covariate effects	df	logLik	AIC _c	ΔAIC_c	Weight
Flea treatment	2	−202.983	410.1	0	0.191
Flea treatment + age	3	−202.509	411.2	1.17	0.106
Flea treatment + season	4	−201.622	411.6	1.55	0.088
Flea treatment + sex	3	−202.781	411.8	1.71	0.081
Null model	1	−205.08	412.2	2.12	0.066

Note: Models including the additional effects of age, season, and sex are not competitive with the top model, despite $\Delta\text{AIC}_c < 2$; these models include uninformative parameters (Arnold 2010).

We converted the estimates of weekly probabilities of den switching to estimates of den residence time (i.e., the expected number of weeks a fox will remain in a den before switching), analogous to calculating life expectancy based on annual survival rates. Adult foxes treated with flea medication were expected to remain in a single den for 4.6 weeks during the pup-rearing season (95% CI = 3.4–6.3; Fig. 3), while the expected residence time for untreated adult foxes during the same time period is 2.9 weeks (95% CI = 2.5–3.7; Fig. 3). Averaged across all ages and seasons, the expected den residence time was 2.1 weeks for untreated foxes and 3.1 weeks for treated foxes.

DISCUSSION

Our study represents the first experimental test of the ectoparasite release hypothesis for a highly mobile carnivore that utilizes multiple dens distributed throughout a landscape. We demonstrated the influence of ectoparasites on the denning behavior of kit foxes; an untested prediction made over 50 yr ago (Egoscue 1962). Specifically, foxes with experimentally reduced flea loads used fewer unique dens per season than untreated foxes (approximately one fewer den per season; Fig. 1) and exhibited higher den use constancy (treated animals were approximately 15% more likely to use the same den in successive weeks and den residence time increased by approximately one week; Figs. 2, 3).

The majority of studies demonstrating impacts of ectoparasites have focused on rodents (Hawlena et al. 2006, Biggins et al. 2010, Hillegass et al. 2010, Zwolak et al. 2013, Archer et al. 2016, Sponchiado et al. 2017) and ungulates (Mooring and Samuel 1999, Vor et al. 2010, Paakkonen et al. 2014, Mysterud et al. 2016). To our knowledge, only two other species of denning carnivores, the European badger (*Meles meles*; Butler and Roper 1996) and black-footed ferret (*Mustela nigripes*; Matchett et al. 2010), have been investigated using an experimental manipulation of ectoparasites. Dissimilar to the species above, kit foxes utilize dens scattered throughout the landscape rather than single den complexes that comprise small spatial extents (Arjo et al. 2003). Our investigation corroborates previous findings that the adoption of a semi-fossorial lifestyle can be

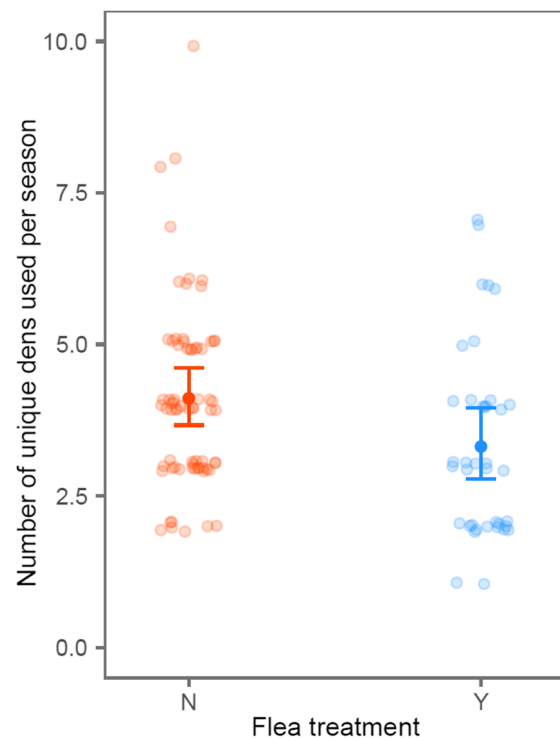


Fig. 1. The effect of flea reduction treatment on the number of unique dens used by kit foxes per season, western Utah, 2010–2013. Semi-transparent points are raw data jittered slightly to allow visualization of overlapping points.

Table 2. Covariate effects appearing in the top five models describing the weekly probability that kit foxes switch dens.

Covariate effects	df	logLik	AIC _c	ΔAIC _c	Weight
Flea treatment + age + season	6	−603.18	1218.4	0	0.27
Flea treatment + age + season + trt × age	7	−603.08	1220.3	1.83	0.108
Flea treatment + age + season + sex	7	−603.18	1220.5	2.03	0.098
Flea treatment + age + season + trt × ssn	8	−602.3	1220.7	2.31	0.085
Flea treatment + season	5	−605.43	1220.9	2.49	0.078
Null	2	−614.55	12333.1	14.67	0

Note: Covariates are abbreviated in interaction effects as Trt (flea treatment) and Ssn (season).

subject to indirect effects, in that spending more time in burrows increases ectoparasite burden, and this burden in turn elicits a behavioral response of modifying den use behavior. Prior to our investigation, reported trade-offs of the burrower lifestyle in canids had been limited to the high energetic costs associated with den construction (Kinlaw 1999).

Notably, all foxes used multiple dens throughout a season, including those with experimentally

reduced flea loads. We suspect this was at least partially attributed to the large territory sizes of kit foxes in our study system, which are among the largest reported for this species (Dempsey et al. 2014). These territories are far larger than individual foxes can travel within a day, necessitating multiple dens within each territory (Bowman et al. 2002, Kluever and Gese 2017). Territory size has been shown to be directly tied to resource availability in kit fox and congener

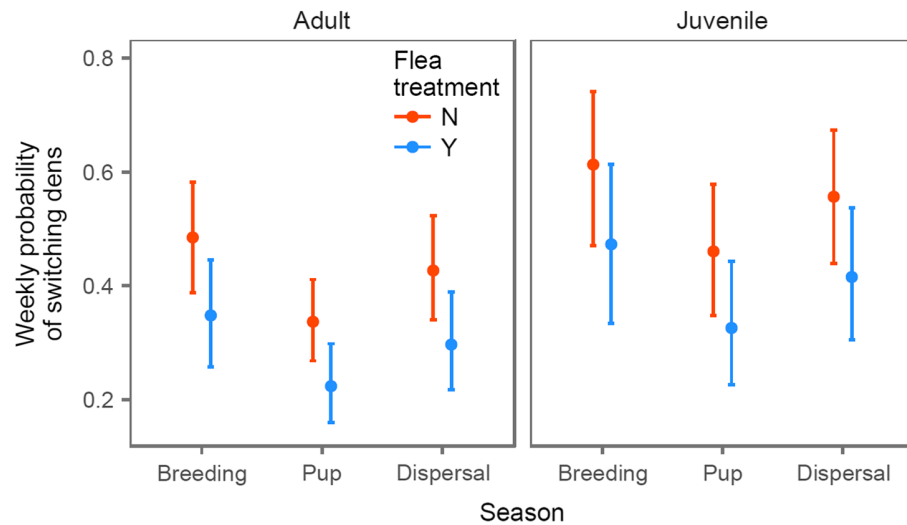


Fig. 2. The effect of flea treatment, season, and age on the weekly probability that a kit fox switches dens, western Utah, 2010–2013.

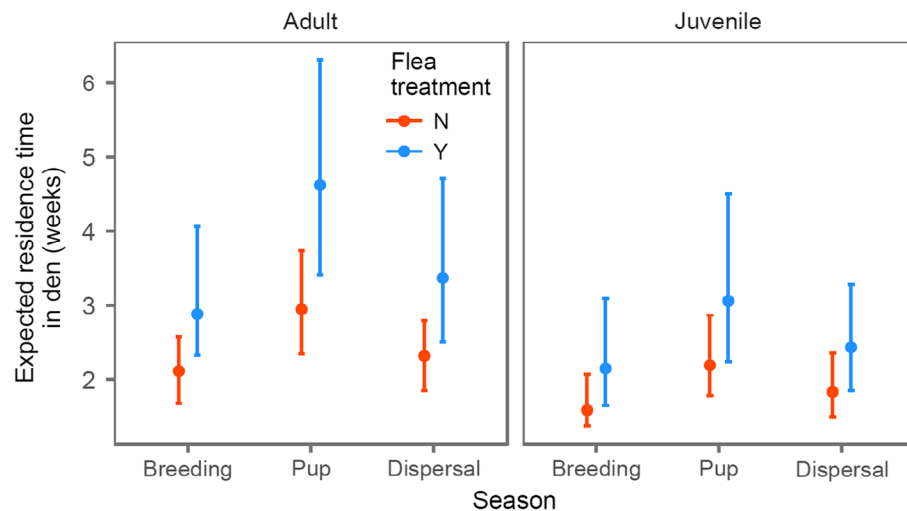


Fig. 3. The effect of flea treatment, season, and age on the expected number of weeks a kit fox will remain in a single den before switching (calculated based on estimates in Fig. 2), western Utah, 2010–2013.

species (White and Ralls 1993, Cypher et al. 2000, Thompson and Gese 2007), and multiple dens are likely required in resource-scarce landscapes such as this desert ecosystem. A noteworthy test to our claim would be to compare kit fox den usage in resource high and low environments. That kit foxes regularly return to dens prior to dusk (Kluever et al. 2013, Kluever and Gese 2017) can largely be attributed to thermoregulatory drivers (Kinlaw 1999). However,

this behavior may also be influenced by predation risk. In the system we investigated, kit foxes are highly susceptible to predation by an exclusively diurnal predator, the golden eagle (*Aquila chrysaetos*; Kluever and Gese 2017). As such, kit foxes would further benefit from being spatially aware of and utilizing a network of dens on the landscape to increase the probability of not engaging in risky diurnal travel in order to return to a den.

Our finding that biological season influences den use constancy (Figs. 2, 3) aligns with previous works on kit foxes (Koopman et al. 1998, Rodrick and Mathews 1999). To our knowledge, we are the first to compare den use constancy for adults and juveniles. These two age classes appeared to be similarly influenced by season (e.g., expected residency time highest during pup-rearing season), but overall residency time was markedly less for juveniles. This finding may be attributed to several factors. First, juveniles often remained spatially affiliated with adults for several weeks or months beyond the pup-rearing season, though observed philopatry was highly variable (B. M. Kluever, *unpublished data*), as has been observed in other canid investigations (Kamler et al. 2004, Gosselink et al. 2010). But, when juveniles foxes did ultimately fully engage in dispersal behavior, they were likely faced with the challenge of locating areas containing suitable resources; it is intuitive that such forays would depress den use residency. Finally, in the system we investigated survival probability for juvenile foxes is markedly less than that of adults (Kluever and Gese 2017) and this likely influenced expected weekly residency times for this age class; an animal cannot re-use the same den if it has expired.

Our finding of flea medication designed for domesticated canids reducing flea loads of kit foxes was not unexpected given its reported effectiveness on domestic canids (Everett et al. 2011, Rohdich et al. 2014). It is also plausible flea burden reductions to kit foxes themselves translated to reductions in utilized dens. Dryden et al. (2011) revealed administering Frontline Plus® to cats and dogs reduced flea populations within contaminated households for up to sixty days. Thus, it stands to reason the presence of treated kit foxes in dens would facilitate a reduction of fleas in the dens themselves. If this is incorrect, our results of treated foxes being more likely to utilize the same dens than untreated foxes are incomprehensible, or at least intractable. However, if Frontline Plus treatments caused physiological stress or effects on diet of our treated foxes, then our finding is perhaps due to animal sickness rather than ectoparasite burden of foxes and dens. Insecticide treatments may cause host stress, lethargy, and lack of appetite, resulting in reduced movement and foraging, which would

explain why treated foxes in our study used dens for prolonged periods (i.e., because they were more ill than non-treated foxes). Though we cannot rule this out as a possibility, visual inspection of foxes during captures and examination of body masses of treated foxes prior to and following treatment do not indicate an illness effect of our treatment, nor has such a condition been reported in other EPRH investigations. Our inclusion of a suite of covariates known to influence kit fox denning behavior (e.g., biological season, sex, age) in our modeling framework lends credence to the interpretation of our findings. Nonetheless, we recommend future works building on our findings employ methods to also quantify flea burden within dens.

We recommend future investigations centered on EPRH expand upon the currently limited taxonomical breadth and strive to determine whether ectoparasite reductions can have additional individual-level effects, such as altering vital rates (e.g., fecundity, survivorship) or population-level effects (e.g., density, occupancy). Examinations of whether field metabolic rates (Kam et al. 2010) or other measures of animal health (Gladalski et al. 2018) change when ectoparasites are reduced are also warranted. If any of the above were found to be true for canids, sustained reductions of ectoparasite burden could have a conservation benefit to imperiled canids, such as the critically endangered San Joaquin kit fox (*Vulpes macrotis mutica*).

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